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PREDATION ON MEXICAN FREE-TAILED BATS BY PEREGRINE FALCONS AND RED-TAILED HAWKS

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Abstract.—We observed Red-tailed Hawks (*Buteo jamaicensis*) and Peregrine Falcons (*Falco peregrinus*) hunting Mexican free-tailed bats (*Tadarida brasiliensis*) during their evening emergence and dawn return at Frio Cave, Uvalde County, Texas in the summer of 1997. Predation by Red-tailed Hawks occurred primarily in the evening (89.5%), and predation by Peregrine Falcons was mostly at dawn (90.5%). In the evening, hawks appeared when large numbers of bats emerged and they attacked at distances >50 m and heights <50 m above the cave. Termination of hunting by hawks in the evening coincided with sunset. In contrast, peregrines hunted for a longer period at dawn when bats returned both in high and low numbers, mostly <100 m of the cave but at various heights. Both species made higher proportions of flights passing by bats without attacking them at dawn (88.9% Red-tailed Hawk and 26.5% Peregrine Falcon) than in the evening (16.4% Red-tailed Hawk and 0% Peregrine Falcon). Hawks had a higher attack rate and capture rate in the evening than at dawn and, in the evening, hawks had a higher capture success than peregrines. At dawn, however, peregrines showed a lower proportion of pass-by flights, a higher attack rate and capture rate, and caught a higher mean number of bats than hawks. Both species were more successful in catching bats after juvenile bats became volant and began foraging. In total, these raptors took 237 bats (96 Red-tailed Hawk and 141 Peregrine Falcon). We estimated the total number of bats taken between mid-April to mid-October to be about 2153 bats which would have accounted for <0.02% of the total colony.

Key Words: *Red-tailed Hawk*; Buteo jamaicensis; *Peregrine Falcon*; Falco peregrinus; *Mexican free-tailed bat*; Tadarida brasiliensis; *predation.*

Depredacion de *Tadarida brasiliensis* por *Falco peregrinus* y *Buteo jamaicensis*

Resumen.—Observamos a *Buteo jamaicensis* y *Falco peregrinus* cazar a *Tadarida brasiliensis* durante el atardecer y amanecer en la Cueva del Frío, Condado de Uvalde, Texas en el verano de 1977. La depredación por *Buteo jamaicensis* ocurrió principalmente en las tardes (89.5%), la depredación por halcones peregrinos ocurrió al amanecer (90.5%). En la tarde, los gavilanes aparecieron cuando numerosos murciélagos emergieron. Estos fueron atacados a mas de 50 mts de distancia y 50 mts de altura sobre la cueva. La caza terminó con el atardecer. En contraste los halcones peregrinos cazaron por un período mas largo al amanecer, cuando los halcones regresaron en mucha y poca cantidad, a menos de 100 mts de distancia de la cueva y a una altura variable. Ambas especies tuvieron una proporción mayor de vuelos razantes sin ataque al amanecer (88.9% para *Buteo jamaicensis* y 26.5% para los halcones peregrinos) en las tardes este porcentaje fué de 16.4% para *Buteo jamaicensis* y 0% para los halcones peregrinos. Los gavilanes tuvieron una tasa de ataque y una captura mas alta en las tardes que al amanecer, en las tardes los gavilanes tuvieron una tasa mayor de captura que los peregrinos. Al amanecer, sin embargo, los halcones peregrinos mostraron una proporción menor de vuelos razantes, una tasa mayor de ataque y captura, y una captura promedio mayor de murciélagos que los gavilanes. Ambas especies fueron mas exitosas en la captura despues de que los murciélagos juveniles comenzaron a forrajear. En total, estas rapaces capturaron 237 murciélagos (96 por parte de *Buteo jamaicensis* y 141 por parte de *Falco peregrinus*). Estimamos un número total de murciélagos capturados entre mediados de abril y mediados de octubre de 2153 lo cual representó el 0.02% del total de la colonia.

[Traducción de César Márquez]

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Bats, being nocturnal, are generally unavailable to diurnal raptors as prey. Most previous records of predation on bats have been for nocturnal raptors (Gillette and Kimbrough 1970, Ruprecht 1979, Barclay et al. 1982, Steyn 1983, Julian and Altringham 1994, Hoetker and Gobalet 1999). Although at least 31 species of diurnal raptors have been observed preying on bats (Gillette and Kimbrough 1970, Sherrod 1978, Cade 1982, Steyn 1983, Byre 1990, Johnsgard 1990), most of them take bats only occasionally, presumably during crepuscular periods and in small proportions relative to their total diets. The specialized Bat Hawk (*Macheiramphus alcinus*) in the Old World tropics is a rare exception because it hunts bats regularly (Black et al. 1979). Speakman (1991) estimated that predation by diurnal raptors accounts for only about 0.57% of the total mortality of British bats. For bats living in large colonies, however, the size of the colony and its predictable behavior (e.g., tendency to emerge early in the evening in high concentrations) may make them conspicuous and potentially-easy prey for opportunistic diurnal raptors (Fenton et al. 1994).

Large numbers of Mexican free-tailed bats (*Tadarida brasiliensis*) reside in the southwestern United States during summer. Colony sizes range from several thousands in man-made structures to tens of millions in some limestone caves. Their evening emergence and dawn return are conspicuous, predictable, and often extend into early morning and late afternoon daytime hours (Davis et al. 1962). Nine species of diurnal raptors from five genera (*Accipiter, Buteo, Circus, Ictinia,* and *Falco*) and two species of owls (Great Horned Owls [*Bubo virginianus*] and Barn Owls [*Tyto alba*]) have been observed to prey on free-tailed bats at their cave localities (Stager 1941, Sprung 1950, Twente 1954, Baker 1962, Taylor 1964, Black 1976, Caire and Ports 1981). Among them, Peregrine Falcons (*Falco peregrinus*) and Red-tailed Hawks (*Buteo jamaicensis*) are the two most common species. The diets of both species in other areas rarely or only occasionally contain bats (Sherrod 1978, Byre 1990, Preston and Beane 1993, Ratcliffe 1993, Cade et al. 1996, Jenkins and Avery 1999). These observations suggest that diurnal raptors can become regular bat predators around large colonies of Mexican free-tailed bats. Nevertheless, the behavior and efficiency of these diurnal raptors in hunting bats, and their predation impact on bat colonies, have not been well-studied.

We document the predation by Peregrine Falcons and Red-tailed Hawks on a large colony of Mexican free-tailed bats during their evening emergence and dawn return. Our goal was to investigate the extent to which these diurnal raptors use bats as food and their hunting efficiency while preying on bats, and to estimate the predation impact on Mexican free-tailed bats. In addition, juvenile Mexican free-tailed bats begin foraging in mid–late July (McCracken and Gustin 1991), and thus the number of bats available to raptors during the emergence and return increases. If raptors capture young, inexperienced, weak, and sick bats in a higher proportion than expected as suggested by Temple (1987) and Simmons et al. (1991), the addition of newly-volant bats in the emergence and return flights might result in a higher capture success by raptors. In this regard, we predicted that compared to early summer, raptors should have a higher capture success in mid–late summer, when inexperienced young bats initiate nightly foraging.

STUDY AREA AND METHODS

Field work took place at Frio Cave (29°25′N, 99°42′W, 354 m elevation), Uvalde County, Texas. The cave is located at the boundary of the southern edge of the Edwards Plateau and the South Texas Plains. One of the largest summer maternity colonies of Mexican free-tailed bats (previously estimated at about 10 million bats; Wahl 1989) inhabits this cave. Major vegetation types surrounding the cave include live oak (*Quercus virginiana*)-mesquite (*Prosopis glandulosa*)-Ash juniper (*Juniperus ashei*)-bluewood (*Condalia hookeri*) parks and mesquite-blackbrush (*Acacia rigidula*) brush (McMahan et al. 1984). These woody plants, mostly less than 10 m high, are scattered in a chaparral-grassland vegetation.

Using binoculars (8×), we observed diurnal raptor predation on Mexican free-tailed bats from 26 May–21 August 1997. In total, we made 23 evening and 23 dawn observations, about once every 3–4 d. The timing of evening and dawn observations was determined based on the activity time of bats (Davis et al. 1962, Lee and McCracken unpubl. data). Evening observations began between 1800–1830 H (Central Standard Time), before the onset of evening emergence of bats, and ended at about 2100–2130 H when it was totally dark. Dawn observations started at about 0430–0500 H, shortly before the dawn return of bats. We stayed at the cave until at least 1000 H, and observations ended at least 30 min after the last bats seen returned. In the evening, we made observations about 30 m from the cave entrance on the top of the hill where the cave is located to maintain a clear view of the moving bat stream. At dawn, returning bats consistently appeared as a column from high altitudes and were easily observable in all directions so we stayed in a lower open area about 50–70 m from the cave entrance. Bats also left and returned to the cave between 2100–0430 H, but in much smaller numbers. We made 12 overnight (from evening to dawn) observations at our evening observation site and detected no raptor activity at the cave during this period. During observations, we moved as little as possible, and constantly used trees and bush as cover to reduce our disturbance to raptors and bats. During each observation period, either one of us would focus on the first raptor that appeared and we would track it until it was last sighted, while the other observer would monitor for the presence of additional raptors.

In each evening or dawn observation period, we recorded the species of each raptor, the time when it was first detected, and the time each raptor was last seen around the cave. We treated each raptor sighting as an independent event without distinguishing individuals of each raptor species. We categorized and timed two types of flights by raptors, pass-by flights and attack flights, and recorded the outcome of each attack flight. A pass-by flight was defined as a raptor flying toward but passing by the emerging or returning bats, without contact with the bat column. An attack flight occurred when a raptor flew into or made contact with the bat column and showed attacking behaviors (e.g., changes in flying posture and speed, partially closed wings, lowering and extending the legs, and partially or fully open and forward toes). We estimated the height from the ground and the distance from the cave of each flight up to 100 m. Flights beyond 100 m in height and distance were estimated in intervals of 50 m. We also estimated the bat density associated with each flight observed. In estimating bat density, because of the large numbers of bats involved, we used the width of cave entrance and relative positions of other surrounding objects (e.g., trees) as reference points when categorizing bat density at any given moment. We categorized bat density into three categories: (1) high, when bats were in a thick emerging or returning column of at least 3 m in diameter, (e.g., more than half of the width of the cave entrance), (2) medium, when bats moved in a narrower column (less than half of the width of the cave entrance) but, at any given moment, they were still too numerous to visually estimate, and (3) low, when the number of bats passing through a reference mark could be estimated at a glance, which was usually less than 50/sec.

Unless otherwise noted, times in min are presented as means (±SE) relative to the times of sunset or sunrise, and sample sizes (*N*) refer to the numbers of evening or dawn observations. All statistical tests used a 0.05 rejection level. We used a simple linear correlation analysis to examine the relationship between times of appearance and departure of raptors with times of sunset, and with times of bat emergence in the evening, respectively. The same method was used to examine the relationship between times of appearance of raptors with times of sunrise, and times of departure of raptors with ending times of returning bats at dawn. We used hunting duration, proportions of pass-by flights, and the following measures to describe hunting efficiency: attack rate (the number of attack flights/min of hunting), capture rate (the number of bats caught/min of hunting), and capture success (%, the number of bats caught relative to the total number of attack flights made) per bird. A Welch-Satterthwaite's approximate t (t', df $= v'$) was used to compare hunting duration, percentage of pass-by flights, and hunting efficiency of raptors between the evening and dawn, and between different raptorial species in the same observation period. This was necessary because of the nonnormality and unequal variances and sample sizes of most of the data sets (Zar 1996). A t-test was used to examine if capture success of raptors differed between the two seasonal periods, before and after juvenile bats began foraging (10–15 July in 1997, Lee unpubl. data). The predation impact by diurnal raptors on bats was estimated by extrapolating data of hunting efficiency over the period when Mexican free-tails are most abundant at caves in southcentral Texas (mid-April–mid-October, Davis et al. 1962). We made this estimation based on an assumption that the numbers of raptors, and the behaviors of raptors and bats remained constant during this period.

RESULTS

Timing and Hunting Behavior. We observed predation on bats by Red-tailed Hawks and Peregrine Falcons at Frio Cave on 17 of 23 evenings (73.9%) and 19 of 23 mornings (82.6%). Red-tailed Hawks were observed on all 17 evenings and Peregrine Falcons were observed on all 19 dawn observations. We observed both species on only two evenings and two mornings (8.7%) and saw no interspecific interactions. We observed 2–4 Red-tailed Hawks simultaneously on 12 of the 17 evenings (71.6%), two Peregrine Falcons on 12 of the 19 mornings (63.2%), but only one Red-tailed Hawk and one Peregrine Falcon at a time in the other evening and dawn observations.

In the evening, the Red-tailed Hawks were first seen at the cave 6.9 ± 4.1 min (N = 17) before sunset and last sighted 11.6 ± 6.3 min (N = 17) after sunset. The time we first saw Red-tailed Hawks did not correlate with the time of sunset ($r^2 = 0.19$, $F_{(1,15)} = 3.22$, $P = 0.09$) and only slightly correlated with the time of the bat emergence ($r^2 = 0.4$, $F_{(1,15)} = 9.27$, $P = 0.009$); however, the times when hawks were last seen correlated with the times of sunset ($r^2 = 0.88$, $F_{(1,15)} = 19.54$, $P < 0.001$; Fig. 1a). We first saw Peregrine Falcons at dawn 16.2 ± 3.2 min (N = 19) before sunrise and last saw them 30.2 ± 5.2 min (N = 19) after sunrise. The time of the first detection of falcons barely correlated with the times of sunrise ($r^2 = 0.33$, $F_{(1,17)} = 7.99$, $P = 0.012$), but their departure times correlated with the ending times of the bat return ($r^2 = 0.89$, $F_{(1,17)} = 70.1$, $P < 0.001$; Fig. 1b). In the two evenings and two mornings when both species were observed, the hawks appeared 6–19 min later than the Peregrine Falcons.

Red-tailed Hawks left perches located 100–150 m either to the east or west of the cave as bats emerged during 47% of the evening observations, but came soaring and gliding into view at other times. When approaching the bats, the hawks flew slowly at 2–3 m above or beside the moving bat stream. When

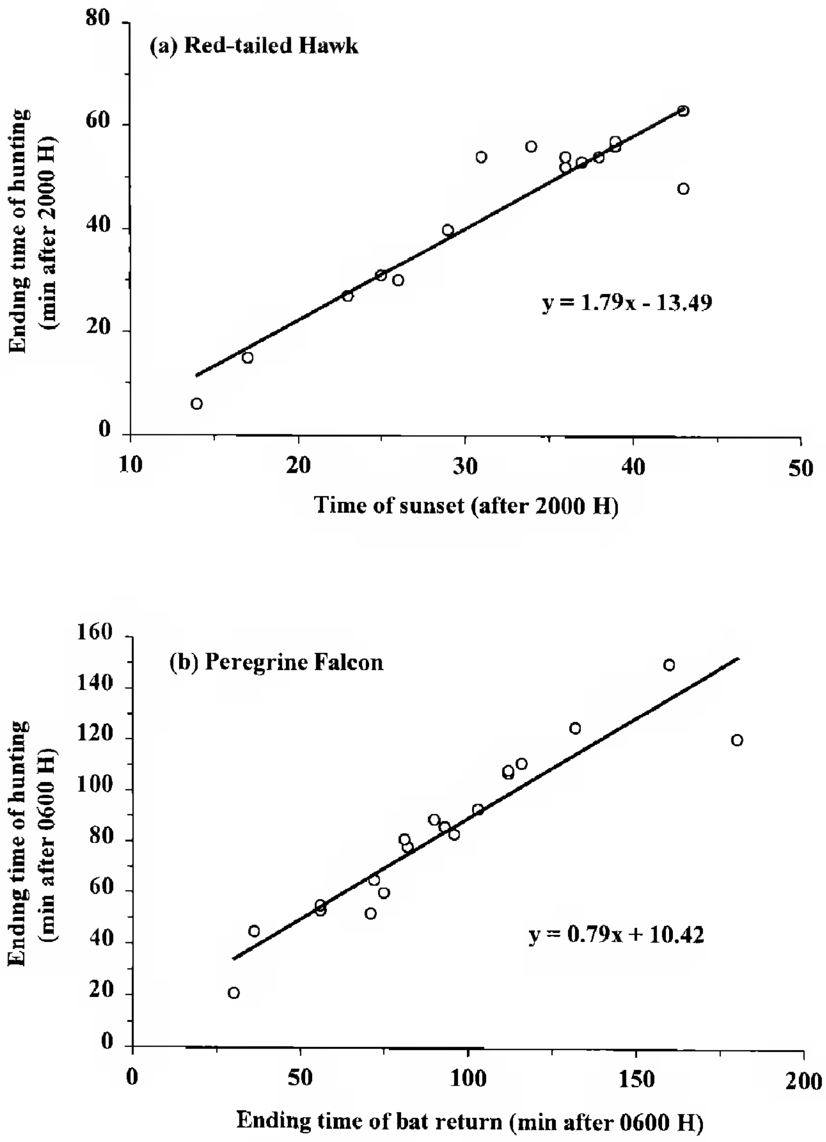

Figure 1. A positive relationship between (a) the ending times of Red-tailed Hawk hunting in the evening and times of sunset and between (b) the ending times of Peregrine Falcons hunting at dawn and the ending times of the return of bats to the cave.

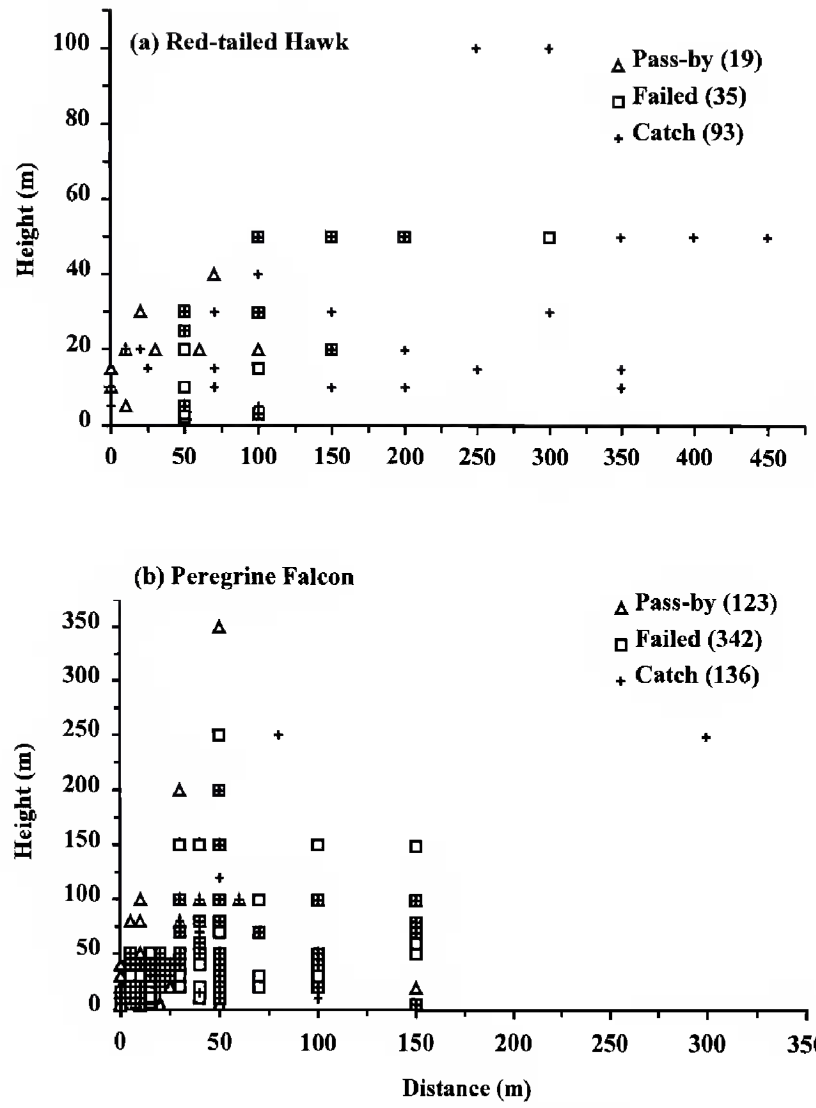

Figure 2. The distribution of pass-by flights, failed attacks, and successful captures by (a) Red-tailed Hawks in the evening and (b) Peregrine Falcons at dawn, over distance and height. Total numbers of each behavior observed are in parentheses. Red-tailed Hawks made their flights at various distances, often >50 m from the cave, but rarely >50 m above the ground. The activity of Peregrine Falcons was concentrated mostly <100 m of the cave, but at heights from near the cave entrance up to 100 m or above.

attacking, a hawk would first set its wings and then lower its legs with open talons and stoop into the bat stream. Upon impact, it would thrust its wings forward for a slight braking effect before flying away from the bat stream. Most pass-by flights occurred within 100 m of the cave at a height of about 50 m. The hawks made a total of 128 evening attacks on 16 evenings ($\bar{x}$ = 3.7 ± 0.7 per bird). Attacks occurred at various distances, often beyond 50 m from the cave, but rarely higher than 50 m above the ground (Fig. 2a). All flights and captures in the evening occurred during periods of high bat density. At dawn, the hawks also flew slowly, but made only two attacks during 10 observed flights catching only one bat. Whether successfully catching a bat or not, the hawks always flew back to perches, often near the pathway of bat stream, before the next attack.

Peregrine Falcons always first appeared at the cave flying. At dawn, they flew straight into the column of bats. At the last moment prior to contact, a falcon would move its legs forward and extend its talons at the bat, while its wings flexed upward. They were observed making a total of 478 dawn attacks on 19 mornings ($\bar{x}$ = 17.4 ± 2.7 per bird). Their activity was concentrated mostly within 100 m of the cave, and at heights from near the cave entrance up to 100 m; however, 3.6% of attacks also occurred above 100 m (Fig. 2b). The highest proportion of pass-by flights (61.3%), attack flights (63.3%), and successful captures (72.8%) occurred during high bat densities at dawn. Peregrine Falcons made only 12 evening attacks, by either angled, direct dives at high speeds, or flying parallel with and then suddenly turning into the bat stream, mostly at 10–50 m from the cave (9 of 12 attacks) and above the cave (11 of 12 attacks). After catching a bat, the falcons would return to perches, one of which was located 200 m north of the cave on a little hill, but often they flew farther across the hill and beyond our observation limit. If an attack failed, the falcons would usually gain altitude after rushing out of the bat column, followed by a semicircular flight either back to their perches or to make another attack.

Hunting Efficiency. On average, each Peregrine Falcon caught 2.5 ± 0.5 bats/evening and 5.0 ± 0.9 bats/morning observation session and each Red-tailed Hawk caught 2.8 ± 0.4 bats/evening and 0.5 ± 0.5 bats/morning observation session. The hunting behaviors and efficiency of each of the two species differed between evening and morning. The falcons spent more time hunting at the cave at dawn than in the evening, but also had a higher proportion of pass-by flights at dawn. The hawks had a higher proportion of pass-by flights, and had a lower mean attack rate, capture rate, and mean bat capture per hawk at dawn than in the evening (Table 1). In the evening, the hawks had a higher capture success ($t' = 3.6$, $v' = 3$, $P < 0.05$) than the falcons. At dawn, however, the falcons had a lower proportion of pass-by flights ($t' = 4.93$, $v' = 15$, $P < 0.05$), a higher attack rate ($t' = 8.29$, $v' = 15$, $P < 0.001$), capture rate ($t' = 4.74$, $v' = 8$, $P < 0.002$), and a higher mean bat capture per raptor ($t' = 4.45$, $v' = 11$, $P < 0.001$) than the hawks. The presence of conspecific raptors engaged in hunting did not affect capture success of the hawks in the evening (single hawk = 80.0 ± 20.0; two or more hawks = 79.7 ± 6.1; $t = 0.02$, df = 14, $P > 0.5$) or the falcons at dawn (single falcon = 23.3 ± 4.3; two falcons = 25.9 ± 5.0; $t = 0.4$, df = 16, $P > 0.4$). Both species, however, showed a higher capture success after juvenile bats became volant and initiated foraging (falcons = 30.9 ± 3.0 and hawks = 87.5 ± 6.1) than earlier in the season (falcons = 12.8 ± 6.1, $t = 3$, df = 16, $P < 0.005$ and hawks = 46.9 ± 15.9, $t = 2.9$, df = 14, $P < 0.01$).

Predation Impact. We observed Peregrine Falcons catching 141 bats (evening = 5 and dawn = 136) and the Red-tailed Hawks catching 96 bats (evening = 95 and dawn = 1). Assuming that the numbers of raptors, and the behaviors of raptors and bats remained constant, and extrapolating the observed levels of predation through the entire season, the total captures of bats by Peregrine Falcons and Red-tailed Hawks at Frio Cave during the peri-

Table 1. Mean (±SE) hunting duration, proportion of pass-by flights, attack rate, capture rate, capture success, and numbers of bats taken by Peregrine Falcons and Red-tailed Hawks during evening and dawn hunting periods. Sample sizes in parentheses refer to the numbers of evening or dawn periods in which predation by each raptor species was sighted. A modified *t*-test (Welch-Satterthwaite's *t'*) was conducted for each measure of each species to compare the hunting efficiency between the two hunting periods.

	Peregrine Falcon					Red-tailed Hawk				
	Evening (2)	Dawn (19)	t'	v'	P	Evening (16)	Dawn (2)	t'	v'	P
Hunting duration (min)	11.5 ± 8.5	45.3 ± 4.3	3.55	2	*	12.4 ± 2.9	23.0 ± 15.0	0.69	1	ns
Pass-by flight (%)	0.0	26.5 ± 6.1	4.37	18	***	16.4 ± 7.0	88.9 ± 11.1	5.53	2	*
Attack rate (attacks/min)	1.15 ± 0.85	0.54 ± 0.06	0.72	1	ns	0.88 ± 0.17	0.03 ± 0.03	4.91	15	***
Capture rate (bats/min)	0.41 ± 0.26	0.14 ± 0.02	1.02	1	ns	0.66 ± 0.13	0.01 ± 0.02	4.97	15	***
Capture success (%)	41.7 ± 8.3	24.9 ± 3.4	1.87	1	ns	79.8 ± 6.5	25.0 ± 25.0	2.12	1	ns
Capture per raptor	2.5 ± 0.5	5.0 ± 0.9	2.47	11	*	2.8 ± 0.4	0.5 ± 0.5	3.49	3	*

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.005$; ns: nonsignificant.

od when large Mexican free-tailed bat colonies inhabit southcentral Texas was estimated as follows:

$$C = D \times P \times R \times T$$

where,
- C = estimated total capture;
- D = total number of days (183 d between mid-April–mid-October);
- P = frequency of appearance (number of evening or dawn observations with raptors present/total number of evening or dawn observations);
- R = mean capture rate (bats/min);
- T = mean hunting duration (min per evening or morning).

From this, we estimated that Red-tailed Hawks consumed a total of 1112 bats (evening = $183 \times 0.74 \times 0.66 \times 12.4 = 1108.3$ bats; dawn = $183 \times 0.09 \times 0.01 \times 23 = 3.8$ bats) and Peregrine Falcons consumed 1041 bats (evening = $183 \times 0.09 \times 0.41 \times 11.5 = 77.7$ bats; dawn = $183 \times 0.83 \times 0.14 \times 45.3 = 963.3$ bats). The total number of bats taken over this period by both species was estimated to be 2153 bats.

DISCUSSION

Timing and Hunting Behavior. Five of the largest known cave colonies of Mexican free-tailed bats exist in an area of about 25 000 km^2 within the Edwards Plateau region (i.e., Bracken Cave [Comal County], Davis Cave [Blanco County], James River Cave [Mason County], Ney Cave [Medina County], and Frio Cave) (Wahl 1989). Predation on bats by Red-tailed Hawks and Peregrine Falcons has been observed at all of these caves (Stager 1941, Sprung 1950, Eads et al. 1957, Baker 1962, Davis et al. 1962, Lee and Kuo pers. obs., McCracken pers. comm.). Apparently, raptors are attracted by these large bat colonies as they emerge or return during daytime and crepuscular periods. Our data show that predation by diurnal raptors on the bats at Frio Cave is a regular event during the summer. Indeed, the frequency of occurrence of Red-tailed Hawks and Peregrine Falcons at Frio Cave is among the highest ever documented for diurnal raptors preying on bat colonies in temperate areas, and is almost comparable to those of Bat Hawks in the Old World tropics (Black et al. 1979). Sprung (1950) reported a similar frequency of occurrence (83.3%) of Red-tailed Hawks, Peregrine Falcons, Sharp-shinned Hawks (*Accipiter striatus*), and Cooper's Hawks (*A. cooperii*), in the evening at Ney Cave, but provided no data on the capture success. Based on observations on six species of diurnal raptors at Carlsbad Caverns National Park, Baker (1962) reported a frequency of occurrence of only 10.2% by Red-tailed Hawks, and <10% for other species, including Sharp-shinned Hawks, Ferruginous Hawks (*Buteo regalis*), Swainson's Hawks (*B. swainsoni*), Northern Harriers (*Circus cyaneus*), and American Kestrels (*Falco sparverius*).

The hunting methods used by Red-tailed Hawks and Peregrine Falcons at Frio Cave were similar to those previously reported (Stager 1941, Sprung 1950, Baker 1962). Differences between the two species in the distribution of activity at various heights, distances, and bat density levels were apparently associated with the behavior of bats at the different times when predation occurred. In the evening, bats emerged and flew as a winding stream at lower heights for at least a few hundred meters beyond the cave; however, at dawn they returned in large numbers as a thick column from high altitudes near or right above the cave entrance (Davis et al. 1962). Bat density at the emergence only began to gradually decline as darkness approached, when the light levels probably also became too dim for diurnal raptors to continue pursuing bats (Fox et al. 1976). Bat densities also gradually declined at dawn, but their return often lasted long after sunrise (Lee and Kuo pers. obs.). A longer bat return at dawn may have provided more opportunities for diurnal raptor hunting because of the increased light levels, even at lower bat densities. Our data on the times of raptor departures and their correlation with times of sunset and ending times of returning bats also provided evidence to support this assumption.

The temporal separation of Red-tailed Hawk and Peregrine Falcon hunting at Frio Cave was intriguing. Rangers at Carlsbad Caverns National Park also found that only 8.8% of total observations had more than one raptor species present hunting Mexican free-tailed bats (Baker 1962), which is compatible with our findings at Frio Cave. It is not known at which time period, habitat types, and food types the Red-tailed Hawks and Peregrine Falcons hunt elsewhere; however, both species occupy diverse habitats, have no particularly preferred hunting period, and eat a variety of prey (Sherrod 1978, Johnsgard 1990, Preston and Beane 1993, Ratcliffe 1993, Cade et al. 1996, Jenkins and Avery 1999). Both species also coexist locally with other raptors in different areas and during different seasons, and each species uses different hunting methods on different occasions (Johnsgard 1990, Ratcliffe 1993).

The temporal separation by the two raptors and the reason why Red-tailed Hawks were mostly observed in the evening and Peregrine Falcons were mostly seen at dawn was probably associated with the eco-morphological characteristics of the raptors and the behavior of bats. Wing loading is one of the most powerful measures to describe and interpret wing morphology and flight performance of flying animals (Norberg 1989). The Red-tailed Hawk has a lower wing loading (0.46–0.56 g/cm^2; Heintzelman 1975), it flies relatively slowly at a ground speed of 30–60 km/hr, and it relies more on a perch-hunting strategy (Preston and Beane 1993). It might be inactive at dawn due to the lack of thermal updrafts (R. Murphy pers. comm.). The Peregrine Falcon, with a relatively high wing loading (0.62–0.91 g/cm^2; Heintzelman 1975), is a fast-flying aerial hunter. It can attain speeds of >100 km/hr in level flight and >250 km/hr in a diving stoop (Ratcliffe 1993). In evenings, bats emerge from caves and fly slowly (40–50 km/hr); however, at dawn they rush into caves from above at almost double the evening speeds (Davis et al. 1962). Presumably, fast-descending bats in the morning are more difficult for Red-tailed Hawks to capture and, instead, they search for prey elsewhere. In contrast, Peregrine Falcons can attack more easily than hawks both in the evening and at dawn because of their superior flight speeds. Thus, the absence of Peregrine Falcons in most of our evening observations demands a closer look at the hunting efficiency of these two raptors in the two hunting periods.

Hunting Efficiency and Predation Impact. The higher proportions of pass-by flights of both raptors at dawn, and the lower attack rate and capture rate of the Red-tailed Hawks at dawn suggest that the hunting of Red-tailed Hawks at dawn was affected by the behavior and fast descending speeds of bats on their return. No previous studies provide comparable data, but Stager (1941) found that it was easier for falcons to catch bats in the evening. Peregrine Falcons hunting at Frio Cave also tended to have a higher mean attack rate, capture rate, and capture success in the evening than at dawn, although the statistical values were not significant, and the power of these tests was low due to the small sample size in the evening. Perhaps falcons hunt more effectively in the evening when bats emerge at slower speeds than at dawn. Their hunting at the cave in the evening might be affected by the presence of larger-sized hawks. Our data cannot verify this speculation because the former was observed hunting on only two evenings and both involved the presence of Red-tailed Hawks. On the other hand, the capture success of Red-tailed Hawks was almost twice that of Peregrine Falcons in the evening. Even though evening hunting by Peregrine Falcons was at least as effective as their dawn hunting, they hunted more often at dawn. This suggested a temporal segregation between Red-tailed Hawks and Peregrine Falcons at an abundant and predictable food resource. Elsewhere, the capture success rates of peregrines vary widely from <5%–>90% depending on the prey types, habitats, and time of the year (reviews in Roalkvam 1985, Dekker 1987, 1988). In most of these studies (18 of 26), however, the capture success rates are lower than what the falcons achieved at dawn at Frio Cave. Roalkvam (1985) concluded that adult Peregrine Falcons in the breeding season have the highest success rate, but their averaged value of 35% was still lower than what Peregrine Falcons achieved in the evening by preying on bats at Frio Cave. Presumably, the extreme abundance and the predictable and conspicuous flight behavior of bats at the cave made them vulnerable and easier to catch than more typical prey (e.g., small- to medium-sized birds). Bat Hawks have a mean capture success rate of only 49.3% in hunting bats from a cave in Zambia (Black et al. 1979).

Fenton et al. (1994) reported success rates of 41.4% for Wahlberg's Eagles (*Aquila wahlbergi*), 50% for Hobby Falcons (*Falco subbuteo*), and 75% for African Goshawks (*Accipiter tachiro*) preying on little free-tailed bats (*Chaerephon pumila*) and Angola free-tailed bats (*Mops condylurus*) at Kruger National Park, South Africa. All these data, however, are from evening observations, and are lower than what the Red-tailed Hawks achieved at Frio Cave. The higher capture success of Red-tailed Hawks at Frio Cave might be due to the earlier and long emergence of Mexican free-tailed bats, which often occurs before sunset (Lee unpubl. data). In Fenton et al. (1994), the bats from small colonies emerged 19–28 min after sunset and emergence only lasted 9.6–20.8 min.

Our data also support the prediction that raptors are more successful in catching bats after juvenile bats initiate nightly foraging with adults. Newly-volant young bats are slower and less agile than adults in flight (Buchler 1980), and may be easier targets for raptors. We have no direct evidence that raptors prey on subadults or juveniles at a higher rate; however, during our dawn observations in late summer, we often saw individual returning bats losing control and free-falling after a failed raptor attack. The similar scene was observed only once during the first half of our field season, before juvenile bats initiated foraging. On three mornings in late July, we searched areas around the cave entrance and found 12 dead or dying bats. These bats showed either evidence of being attacked by raptors (e.g., wounds on abdomen and exposed digestive tracts), broken wings, or blood on their nostrils, and all were subadults.

From the mean daily bat consumption per bird (falcons = 5 bats at dawn; hawks = 2.8 bats in the evening) and a mean body mass of 13 g for Mexican free-tails ($N = 3021$; Lee unpubl. data), we estimated that, each day, a Peregrine Falcon ate 65 g of bats at dawn and a Red-tailed Hawk ate 36.4 g of bats in the evening. Daily food requirements of Peregrine Falcons and Red-tailed Hawks in the summer are about 11.5% and 8.6% of their body mass, respectively (Brown and Amadon 1968). This translates to 52.1–78.8 g of food for a male and 82.7–125.8 g of food for a female Peregrine Falcon, and 59.3–111.8 g of food for a male and 77.4–125.6 g of food for a female Red-tailed Hawk. Thus, by hunting only bats, the Peregrine Falcons and Red-tailed Hawks at Frio Cave could have met 51.7–124.8% and 29–61.4% of their respective daily food requirements in the summer. These values may be overestimated because raptors may not consume prey entirely (Simmons et al. 1991), and we made no attempts in searching nest sites and prey remains of these raptors. Nonetheless, it suggests that these large bat colonies still represent a fairly important food resource to diurnal raptors. On the other hand, the estimated total of 2153 bats killed by diurnal raptors over a period of six months, is only 0.02% of the estimated population size of Mexican free-tails during the summer at Frio Cave. The actual mortality due to raptor predation may also have been underestimated, because many bats that died as a consequence of raptor attacks were not captured. Nevertheless, predation by diurnal raptors would appear to contribute only a small part of the estimated, overall annual mortality rate of 20–30% for this species (Davis et al. 1962).

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